

**Abstract**—I simulated somatic growth and accompanying otolith growth using an individual-based bioenergetics model in order to examine the performance of several back-calculation methods. Four shapes of otolith radius-total length relations (OR-TL) were simulated. Ten different back-calculation equations, two different regression models of radius-length, and two schemes of annulus selection were examined for a total of 20 different methods to estimate size at age from simulated data sets of length and annulus measurements. The accuracy of each of the twenty methods was evaluated by comparing the back-calculated length-at-age and the true length-at-age. The best back-calculation technique was directly related to how well the OR-TL model fitted. When the OR-TL was sigmoid shaped and all annuli were used, employing a least-squares linear regression coupled with a log-transformed Lee back-calculation equation ( $y$ -intercept corrected) resulted in the least error; when only the last annulus was used, employing a direct proportionality back-calculation equation resulted in the least error. When the OR-TL was linear, employing a functional regression coupled with the Lee back-calculation equation resulted in the least error when all annuli were used, and also when only the last annulus was used. If the OR-TL was exponentially shaped, direct substitution into the fitted quadratic equation resulted in the least error when all annuli were used, and when only the last annulus was used. Finally, an asymptotically shaped OR-TL was best modeled by the individually corrected Weibull cumulative distribution function when all annuli were used, and when only the last annulus was used.

## An evaluation of back-calculation methodology using simulated otolith data

**Michael J. Schirripa**

Hatfield Marine Science Center  
Northwest Fisheries Science Center  
2030 SE Marine Science Drive  
Newport, Oregon 97365-5296  
E-mail address: Michael.Schirripa@noaa.gov

The average rate of growth of an individual fish in a population is critical to age-based stock assessments. The average rate at which the fish within the stock increases in weight ultimately determines the level of effort required to extract a desired yield from the stock as a whole (Ricker, 1975). Furthermore, current conservation standards (Gulland and Boerema, 1973; Goodyear, 1993) are dependent upon the rate of individual growth. Thus, errors in the estimation of growth can lead to erroneous advice to fishery managers concerning the present and possible future status of a population.

By far the most common method of estimating fish growth rate is by estimating the age of individual fish from calcified structures (scales, otoliths, spines, etc.); but for this study, however, otoliths were considered the representative hard structure) and with the subsequent assumption that these fish are an unbiased representation of size at that age. Growth is then described as the change in weight or length over some unit of time. To standardize age at which size is estimated, or to obtain length-at-age data on ages not included in the sample, back-calculation techniques are often employed to estimate a fish's size at a previous age (Bagenal, 1978). The process of back calculation can be broken down into three steps: verification of the periodicity of annulus formation, establishment of an otolith radius-total body length (OR-TL) relation, and the estimation of size at the time of annulus formation. In this study, I used simulations to examine how the establishment of the OR-TL relation and the form of the back-calculation equation used may influence growth rate estimates made from otoliths.

The back-calculation process assumes that somatic growth is directly related to otolith growth (Bagenal, 1978). This assumption is usually validated through the demonstration of a relationship between the otolith radius and body length by a least-squares regression of body length on otolith radius. A variation of this technique uses a functional (model II) regression, based on the assertion that neither body length nor otolith radius are truly independent (i.e. measured without error) (Ricker, 1973, Laws and Archie, 1981). Uncertainties can enter this process from several sources. For example, incomplete data can make it difficult to discern if this relationship is linear. Furthermore, using regression to estimate beyond the range of the data is not recommended. Estimating beyond the range of the data can become a problem when back-calculating to very early ages that are not represented in the sample. Furthermore, several studies have found that otolith growth and somatic growth can be uncoupled (Mosegaard et al., 1988; Reznick et al., 1989; Secor and Dean, 1989; Wright et al., 1990; Milicich and Choat, 1992; Secor and Dean, 1992). Hales and Able (1995) found that changes in somatic growth accounted for only half of the variation in otolith growth. This uncoupling of somatic and otolith growth rates challenges the assumption that back-calculation is based on.

The question of what is the proper back-calculation equation to use is a question that has received considerable attention. Bagenal (1978) discussed three separate methods and suggested that a combination of methods might be helpful in some cases. Francis (1990) presented an in-depth review of

six different back-calculation equations and their use. Ricker (1992) later commented on the conclusions of Francis (1990) to suggest yet another variation on the method. Further variation exists on exactly which combination of annuli to use. Standard method suggests the use of all available annuli within the otolith to increase sample size. However, recent literature (Vaughan and Burton, 1994), as well as older reports (Ricker, 1973), have suggested that only the most recently formed annuli should be used. A review of the literature on age and growth shows that a variety of techniques are in use today and that there is no real agreement on a definitive method. The purpose of this study was to examine how well the various back-calculation techniques accurately estimate lengths at previous ages and to examine the biases associated with each technique.

## Methods

### Model structure

I simulated somatic and otolith growth using a bioenergetics model. A detailed description of the model is presented in Schirripa and Goodyear (1997). The life history and growth parameters were calibrated to fit, as closely as possible, to reported estimates of striped bass growth (Bason<sup>1</sup>); however the model is not intended to be a striped bass model *per se*. Because of the commercial and recreational importance of striped bass, a great body of literature from the field and laboratory work is available. One of the most studied populations of striped bass is that of the Chesapeake Bay system (Cohen et al., 1983; Coutant et al., 1984; Goodyear, 1984, 1985; Tuncer, 1988; Coutant and Benson, 1990; Secor, 1992; Brandt and Kirsch, 1993; Rose and Cowan, 1993; Rutherford and Houde, 1995; Secor and Houde, 1995). Biological and environmental parameters reported for the populations of this system were used whenever possible. The growth model used an individually based framework, but rather than following every fish of the cohort singly, "cells" of fish with identical attributes were followed instead (Rose et al., 1993). A total of 250 cells, each with eleven attributes, were modeled. Attributes examined included age, length, biomass, daily food ration, food conversion efficiency, otolith weight, otolith radius, maximum length attained, maximum biomass attained, brain weight, condition factor, and number of fish that the cell represented.

The term "population" is used to define those fish that remained alive for the entire simulation, unaffected by either natural or fishing mortality. The term "catch" refers to the entire group of fish that were susceptible and killed due to fishing mortality, and "sample" refers to a subsample of individuals from the catch, selected on the

basis of length and frequency within the catch. Frequency in the catch was a function of the selectivity of the gear under consideration and frequency in the population. For the purposes of this study, gear was considered nonselective. Annulus formation within the otolith was assumed to occur at the end of every growth year and to be measured without error.

The specific somatic growth rate of an individual fish was calculated by a balanced energy equation. Equations for rates of consumption, respiration, egestion, and excretion generally followed those given by Hewett and Johnson.<sup>2</sup> The otolith growth model used was a modification of the equations presented by Mosegaard.<sup>3</sup> Fish formed an otolith when they reached 90 mm in length. Daily change in otolith weight ( $O_w$ ) was modeled as a function of daily change in either brain weight ( $B_w$ ) or brain length ( $B_l$ ). In the case of brain weight, weight specific brain growth rate was modeled as a function of the somatic growth rate as follows

$$\text{Growth.Brain} = \text{Growth.Somatic} \times a_2, \quad (1)$$

where  $a_2$  = less than 1, denoting that brain growth rate is slower than somatic growth rate.

The change in  $B_w$  then was calculated as

$$dB_w/dt = \text{Growth.Brain} \times B_w. \quad (2)$$

The daily change in otolith weight was then calculated as

$$dO_w/dt = a_4 \times \text{Brain.weight} \times \text{temp}^{a_1}, \quad (3)$$

where  $a_4$  = the conversion factor from brain weight to otolith weight (see below);

$\text{temp}$  = the average temperature for the day in degrees centigrade; and

$a_1 = 0.77$ , which is used to determine the overall size of the otolith.

Otolith radius,  $O_r$ , was then calculated from  $O_w$  assuming a spherical shape as

$$O_r = \frac{O_w}{SpD} \times (3/4\pi)^{0.333}, \quad (4)$$

where  $SpD = 2.5$  and is the specific density of the otolith.

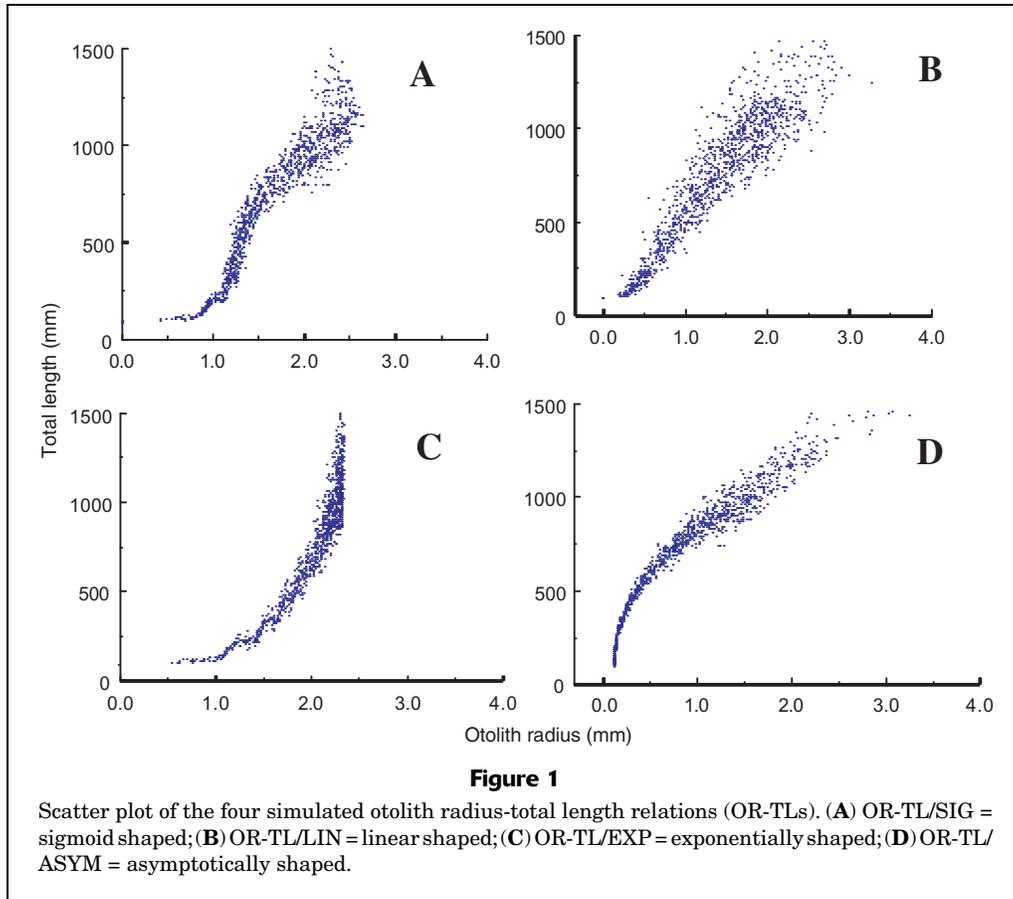
Assuming a spherical shape resulted in a unique radius for a given weight (i.e. a sphere made it unnecessary to consider otolith length).

When brain length was used to model otolith radius,  $B_w$  was calculated as in Equation 2 and  $B_l$  was calculated as the cube root of  $B_w$ :

<sup>1</sup> Bason, W. H., S. E. Allison, L. O. Horseman, W. H. Keirse, P. E. LaCivita, R. D. Sander, and C. A. Shirey. 1976. Ecological studies in the vicinity of the proposed Summit Power Station January through December 1975. Vol. 1, Fishes, 392 p. Ichthyological Associates, Ithaca, NY.

<sup>2</sup> Hewett, S. W., and B. L. Johnson. 1992. Fish bioenergetics model 2. Sea Grant Institute, Technical Report WIS-SG-92-250, 79 p. University of Wisconsin, Madison, WI.

<sup>3</sup> Mosegaard, H. 1994. A model of otolith and larval fish growth. In ICES, Report of the working group on recruitment processes, C.M. 1994/L:12, p. 34-38.



$$B_1 = B_W^{0.333}. \quad (5)$$

$O_r$  was then calculated as

$$O_r = B_1 \times 0.5. \quad (6)$$

### Otolith radius-total length relation

The OR-TL relation was fitted as closely as possible to that reported for striped bass by Heidinger and Clodfelter (1987). Modeling the conversion factor  $a_4$  (Eq. 3) as a function enabled me to generate four different OR-TL relations typically found in nature. A sigmoid shaped OR-TL (OR-TL/SIG) relation (Fig. 1A) relation was achieved by setting the parameter  $a_2 = 0.08$  and modeling the parameter  $a_4$  as a function of body length:

$$a_4 = 9 + (-7 \times \sin(0.006 \times \text{Length}) + 5). \quad (7)$$

A linear shaped OR-TL (OR-TL/LIN) relation (Fig. 1B), as found in striped bass (Heidinger and Clodfelter, 1987) was achieved by setting the parameter  $a_2$  (from Eq. 1) to 0.85 and modeling otolith radius as a function of brain length (the parameter  $a_4$  was not necessary for this relation). An exponential OR-TL (OR-TL/EXP) relation (Fig. 1C), similar to that found for vermilion snapper, *Rhomboplites aurorubens*, (Grimes, 1978) was achieved by again setting

the parameter  $a_2$  to 0.08 and modeling the parameter  $a_4$  as a linear function of otolith weight:

$$a_4 = 25 - (1.75 \times O_W). \quad (8)$$

An asymptotic OR-TL (OR-TL/ASYM) relation (Fig. 1D), similar to that found for walleye, *Stizostedion vitreum*, (Heidinger and Clodfelter, 1987), was achieved by keeping the parameter  $a_2 = 0.08$  and modeling the parameter  $a_4$  as a function of total length:

$$a_4 = 8.717E - 12 \times \text{Length}^4. \quad (9)$$

### Mortality

Mortality could occur from three sources: direct starvation, random natural mortality based on length, and fishing mortality. If a fish lost more than a specified percentage of its maximum attained body weight (35% for larvae and 50% for juveniles), it died from starvation. Fishing mortality was described first as an overall value ( $F=0.4$ ) and then divided by 365 to calculate a daily value. In order to ensure that there would be no sampling bias due to gear selectivity, fishing mortality was assumed to be nonselective (random).

The four simulated OR-TL relations were described by using four different functions: 1) ordinary least squares (OLS) linear regression (model I)

**Table 1**

The ten back-calculation and OR-TL regression equations evaluated in this study. Method number refers to all annulus/last annulus only.  $L_n$  is the estimated length at formation of annulus  $R_n$ ;  $L_c$  and  $R_c$  is total length of fish and otolith radius at capture, respectively. OLS = ordinary least squares.

Method	Back-calculation equation	OR-TL fitting method
1/11	$L_n = (R_n / R_c) L_c$	none
2/12	$L_n = a + (bR_n)$	OLS linear regression
3/13	$L_n = a + (R_n / R_c) (L_c - a)$	OLS linear regression
4/14	$L_n = a + (bR_n)$	functional linear regression
5/15	$L_n = a + (R_n / R_c) (L_c - a)$	functional linear regression
6/16	$\log_e(L_n) = \log_e(a) + b(\log_e(R_n))$	OLS linear regression with log transformation
7/17	$\log_e(L_n) = \log_e(L_c) + b(\log_e(R_n) - \log_e(R_c))$	OLS linear regression with log transformation
8/18	$L_n = K(1 - \exp(-(R_n / \alpha)^\beta))$	Weibull cumulative function
9/19	$L_n = c + (dR_n) + (eR_n^2) + (fR_n^3)$	quadratic equation
10/20	$L_n = (K(L_c / L_p)) (1 - \exp(-(R_n / \alpha)^\beta))$	Weibull cumulative function

$$L_c = a + R_c b, \tag{10}$$

where  $L$  = the total length; and  $R$  = the otolith radius and represents the independent variable (assumed to be measured with out error); 2) functional regression (model II), which has the identical formula as Equation 10 but does not assume an independent variable (i.e. both  $L$  and  $R$  are measured with error); 3) Weibull cumulative function (Weibull, 1951),

$$L_c = K \left( 1 - \exp \left[ - \left( \frac{R_c}{\alpha} \right)^\beta \right] \right), \tag{11}$$

and 4) a third order quadratic equation

$$L_c = c + (d_1 R_c) + (e_2 R_c^2) + (f_3 R_c^3). \tag{12}$$

These four functions were fitted with the SAS NLIN procedure (SAS, 1988).

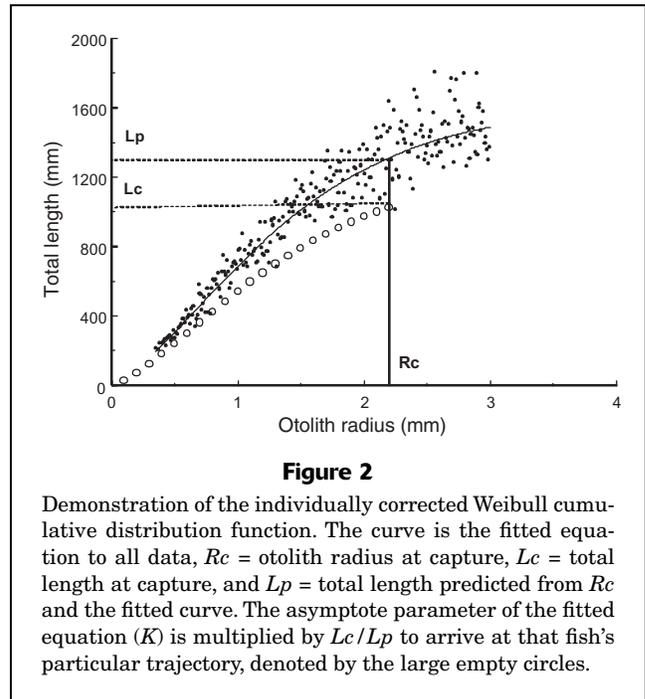
Ten combinations of the back-calculation formula and OR-TL fitting procedures were used (Table 1). Methods 1 through 9 were simple derivations from a standard regression equation and required only a fitting of the parameters and substitution into the equation (Bagenal, 1978). Method 10 however used a derivation of the Weibull distribution function. In this method, the parameter defining the asymptotic limit of the function ( $K$ ) was modified by  $L_c/L_p$  as

$$L_n = \left( K(L_c / L_p) \right) \left( 1 - \exp \left[ - \left( \frac{R_c}{\alpha} \right)^\beta \right] \right), \tag{13}$$

where  $L_p$  = the theoretical length of the fish according to its otolith radius as predicted by the fitted OR-TL Weibull function; and

$L_c$  = the actual length at capture.

If, for instance, the actual length of the fish was less than the theoretical length ( $L_c/L_p$  is less than 1), the parameter



$K$  was corrected downward and subsequent back-calculations for that fish were made according to its own individual trajectory (Fig. 2). In this way,  $L_c/L_p$  was calculated for each individual fish in the same way that the slope of the Fraser-Lee back-calculation equation was estimated for each fish. These ten combinations were used for all available annuli and then repeated by using the last annulus only, for a total of twenty different methods.

As a measure of bias, the back-calculated length at age 2 was regressed on the age of the fish from which the estimate came (source age). In this way, for instance, a strong "Lee's phenomenon" (the phenomenon that back-calculated lengths for a given age group become smaller as

Table 2

Age (yr)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	<i>n</i>
Age and calculated true mean length-at-age (mm) for a typical simulated population.															
1	102	—	—	—	—	—	—	—	—	—	—	—	—	—	250
2	108	208	—	—	—	—	—	—	—	—	—	—	—	—	250
3	108	208	330	—	—	—	—	—	—	—	—	—	—	—	250
4	108	208	329	457	—	—	—	—	—	—	—	—	—	—	250
5	107	207	329	457	573	—	—	—	—	—	—	—	—	—	250
6	107	207	329	457	572	674	—	—	—	—	—	—	—	—	250
7	107	207	329	457	572	674	763	—	—	—	—	—	—	—	250
8	108	207	329	457	574	676	766	845	—	—	—	—	—	—	250
9	108	208	330	459	576	679	769	849	917	—	—	—	—	—	250
10	108	208	330	460	578	681	772	853	921	980	—	—	—	—	250
11	108	208	331	460	577	680	771	852	920	981	1032	—	—	—	250
12	108	208	331	460	577	680	771	851	920	980	1031	1077	—	—	250
13	109	208	331	460	578	681	772	853	920	980	1031	1076	1115	—	250
14	109	208	331	459	577	678	769	849	916	974	1025	1070	1108	1139	250
Mean	104	208	330	458	575	677	768	850	918	978	1029	1073	1110	1138	
Age and calculated true mean length-at-age (mm) for a typical simulated catch.															
1	102	—	—	—	—	—	—	—	—	—	—	—	—	—	117
2	109	207	—	—	—	—	—	—	—	—	—	—	—	—	105
3	108	207	323	—	—	—	—	—	—	—	—	—	—	—	101
4	108	208	323	448	—	—	—	—	—	—	—	—	—	—	86
5	108	205	321	449	572	—	—	—	—	—	—	—	—	—	93
6	107	205	319	445	567	673	—	—	—	—	—	—	—	—	95
7	108	206	323	448	569	676	765	—	—	—	—	—	—	—	98
8	107	206	322	450	572	680	771	853	—	—	—	—	—	—	104
9	108	207	323	449	571	679	771	853	918	—	—	—	—	—	115
10	108	205	318	443	562	665	755	834	901	962	—	—	—	—	105
11	109	206	320	442	561	667	757	836	903	964	1016	—	—	—	106
12	107	204	316	438	557	661	751	831	901	964	1017	1060	—	—	102
13	107	204	315	439	559	664	756	838	908	973	1027	1071	1107	—	101
14	108	203	316	442	563	670	763	844	910	970	1021	1061	1096	1127	88
Mean	106	206	321	446	567	672	763	843	908	966	1020	1064	1102	1127	

the fish from which they are calculated become older) or a similar effect would result in a negative slope. If there is no bias caused by this approach, the expected value of this slope is zero when randomly sampled from an unfished population.

The accuracy of each of the twenty methods of back-calculation was evaluated by plotting the percent error of the estimated length-at-age in relation to the true value. As an overall evaluation of the method, a sum-of-squares (SS) was calculated by squaring the percent error between the estimated length-at-age and the true length-at-age and summing across all ages.

## Results

The true underlying mean length-at-age of both the surviving population and the catch (Table 2) was calculated and tabulated in standard back-calculation type tables. There was no apparent trend in the estimates as a func-

tion of the age used in the back-calculation. This lack of trend, and the high degree of similarity between the mean length-at-age of the population and catch suggested that the catch was a random and representative sample of the population.

Methods 2, 4, 6, 8, and 9 resulted in the least bias and method 1 the most bias when the slopes were examined across the various shapes of the OR-TL relation (Fig. 3). The linear shaped OR-TL (OR-TL/LIN) relation resulted in the least amount of bias, and the exponential shaped OR-TL (OR-TL/EXP) relation resulted in the most when the various relations were examined across methods.

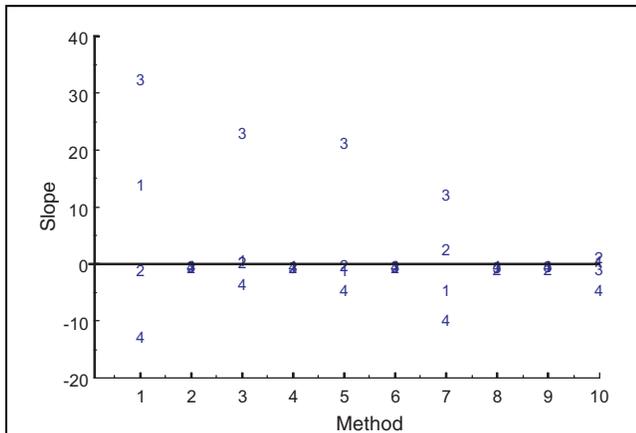
### Sigmoid-shaped OR-TL relation

Of the four functions fitted to the OR-TL/SIG relation (Table 3), the Weibull cumulative function resulted in the highest coefficient of determination ( $r^2=0.914$ ); however the coefficient of determination of the quadratic fit was very similar ( $r^2=0.913$ ).

**Table 3**

Summary of the combination of OR-TL and back-calculation models that resulted in the best lack-of-fit (lowest sum of squares [SS]) for each of the four shapes of OR-TL examined

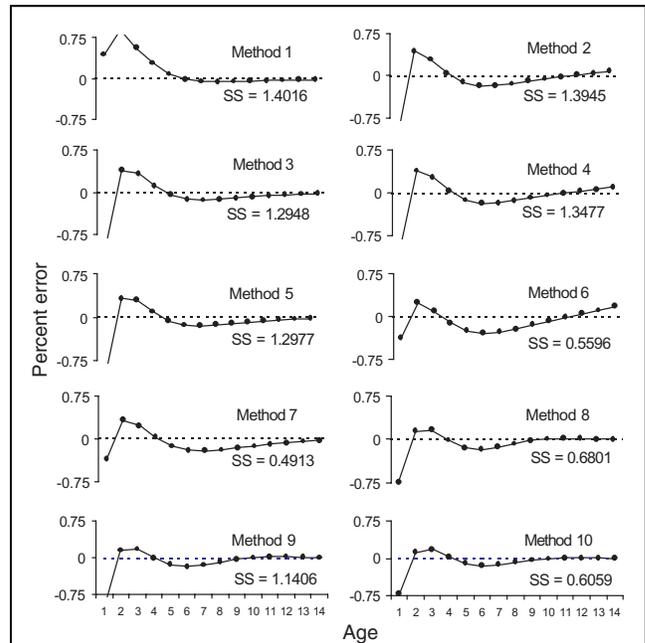
OR-TL shape	Best lack-of-fit result	
	OR-TL model	Back-calculation model
<b>Sigmoid</b>		
All annuli	linear regression, model I	$\log_e(L_n) = \log_e(L_c) + b(\log_e(R_n) - \log_e(R_c))$
Last annulus only	none	$L_n = (R_n / R_c) L_c$
<b>Linear</b>		
All annuli	linear regression, model II	$L_n = a + (R_n / R_c)(L_c - a)$
Last annulus only	linear regression, model II	$L_n = a + (R_n / R_c)(L_c - a)$
<b>Exponential</b>		
All annuli	quadratic equation	$L_n = c + (dR_n) + (eR_n^2) + (fR_n^3)$
Last annulus only	quadratic equation	$L_n = c + (dR_n) + (eR_n^2) + (fR_n^3)$
<b>Asymptotic</b>		
All annuli	Weibull cumulative function	$L_n = (K(L_c / L_p))(1 - \exp(-(R_n / \alpha)^\beta))$
Last annulus only	Weibull cumulative function	$L_n = (K(L_c / L_p))(1 - \exp(-(R_n / \alpha)^\beta))$



**Figure 3**

Scatterplot of the slopes of the regression of back-calculated length at age 2 versus age at capture for the ten back-calculation methods that used all annuli. The numbers plotted indicate the shape of the OR-TL relation examined (1=OR-TL/SIG [sigmoid], 2=OR-TL/LIN [linear], 3=OR-TL/EXP [exponential], 4=OR-TL/ASYM [asymptotic]).

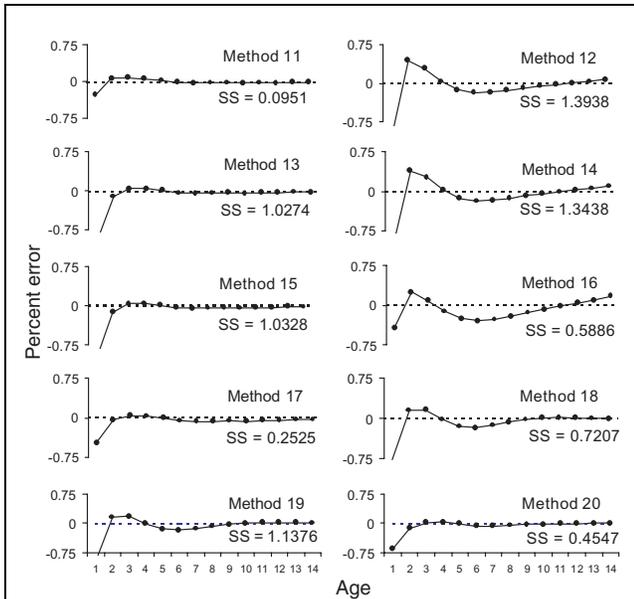
The sigmoid shape of the OR-TL relation was evident in the shape of the percent error plots for methods 1 through 10 (Fig. 4). When the OR-TL relation was sigmoid-shaped and all annuli were used, the least error resulted from employing a ordinary least-squares regression coupled with the log-transformed Fraser-Lee back-calculation equation (method 7, SS=0.4913). The greatest error appeared when using the direct proportion equation (Fig. 4, method 1, SS=1.4016). Using the y-intercept of the OR-TL relation in the back-calculation equation (methods 3/13 and 5/14



**Figure 4**

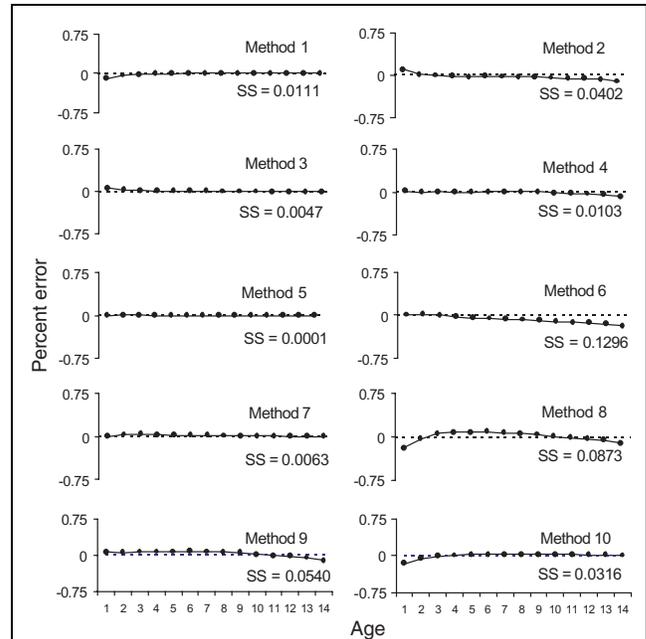
Error in mean length at age estimates using all annuli and the ten back-calculation methods outlined in Table 1 for the sigmoid-shaped OR-TL relation. SS = sum of squares.

in Table 1) had little effect on the total sum of squares when comparing method 2 with method 3; in addition, correcting for different limits of the Weibull function in methods 8 versus 10 had little effect. However, the log transformation of methods 6 and 7 reduced the sum of squares considerably.



**Figure 5**

Error in mean length at age estimates using the last annulus only and the ten back-calculation methods outlined in Table 1 for the sigmoid-shaped OR-TL relation. SS = sum of squares.



**Figure 6**

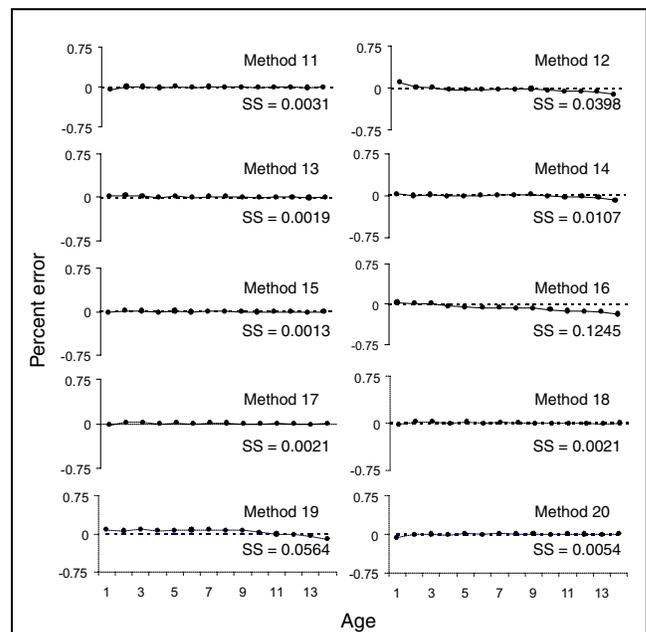
Error in mean length at age estimates using all annuli and the ten back-calculation methods outlined in Table 1 for the linear-shaped OR-TL relation. SS = sum of squares.

The sigmoid shape of the OR-TL relation was not as evident in the shape of the percent error plots for methods 11 through 20 (Fig. 5). When only the last annulus was used, the least error resulted from employing a direct proportionality back-calculation equation (Fig. 5, method 11, SS=0.0951), and the greatest error from using direct substitution into the OLS regression equation (Fig. 5, method 12, SS=1.3938). When only the last annulus was used with comparable back-calculation equations, as in methods 12 versus 13 and 18 versus 20, both the sum of squares and bias were reduced considerably.

**Linear-shaped OR-TL relation**

Of the four functions fitted to OR-TL/LIN, the ordinary least squares and functional linear regressions resulted in the highest coefficient of determination value ( $r^2=0.916$ ). The curvature of the Weibull and quadratic fits showed that the relation deviated slightly from a straight line.

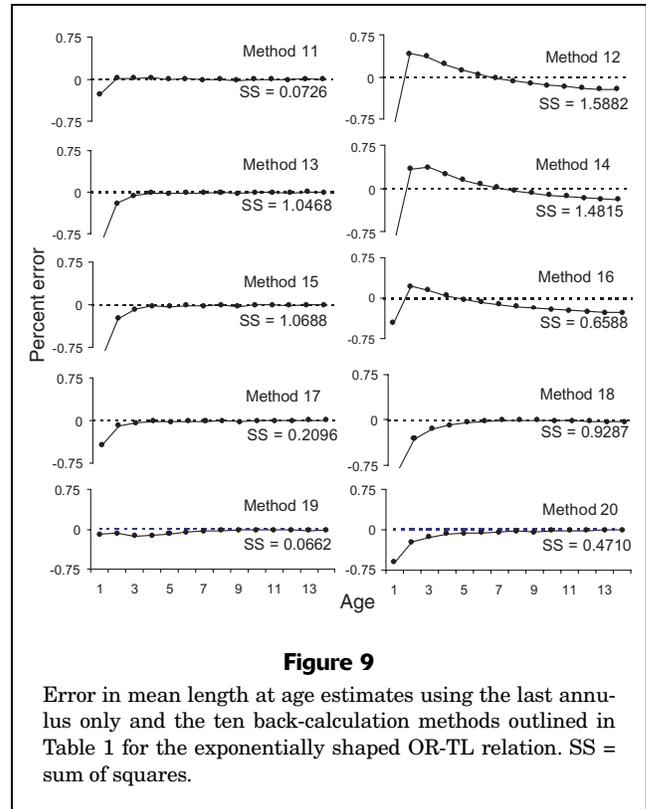
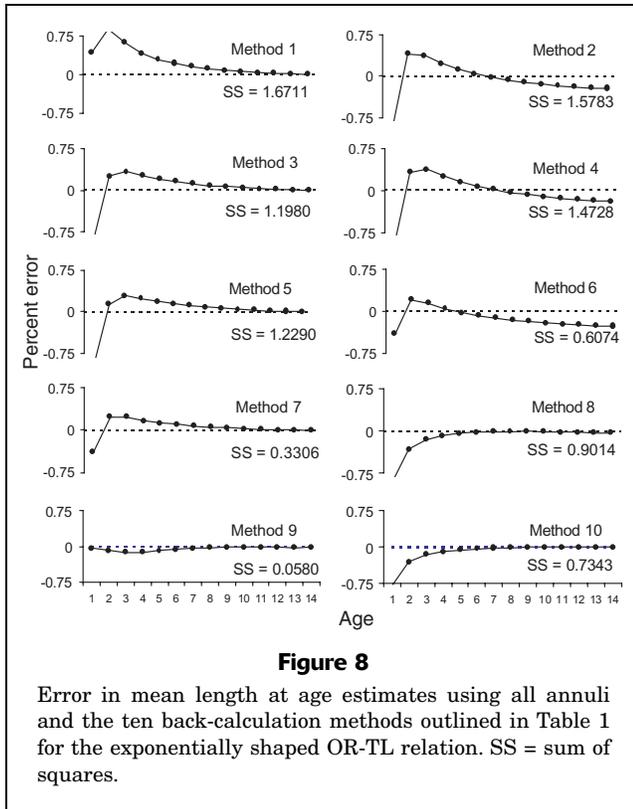
There was a high degree of similarity between the percent error plots for all twenty methods (Figs. 6 and 7), suggesting that the estimation of length-at-age is not as sensitive to the method of back-calculation when the OR-TL relation is linear as when it is curved. When the OR-TL relation was linear, the least error resulted from employing a functional regression coupled with the Fraser-Lee back-calculation equation when all annuli were used (Fig. 6, method 5, SS=0.0001) and when only the last annulus was used (Fig. 7, method 15, SS=0.0013). The greatest error resulted from direct substitution into the OLS regression following a natural log transformation of all parameters, both when all



**Figure 7**

Error in mean length at age estimates using the last annulus only and the ten back-calculation methods outlined in Table 1 for the linear-shaped OR-TL relation. SS = sum of squares.

annuli were used (Fig. 6, method 6, SS=0.1296) and when only the last annulus (Fig. 7, method 16, SS=0.1245).



### Exponentially shaped OR-TL relation

Of the four functions fitted to OR-TL/EXP, the quadratic function resulted in the highest coefficient of determination ( $r^2=0.883$ ); however the coefficient of determination of the Weibull function fit was nearly as high ( $r^2=0.878$ ). The percent errors, when using all annuli and linear regression, followed a pattern similar to the residuals of the OR-TL relation (Fig. 8). This trend was also evident, although not as strong, when only the last annulus was used (Fig. 9). Using the quadratic function rather than the linear regression to fit the OR-TL relation did the most at removing this bias (Fig. 8 method 9, and Fig. 9 method 19).

When the OR-TL relation was exponentially shaped and all annuli were used, the least error resulted from direct substitution into the fitted quadratic equation (Fig. 8, method 9, SS=0.0580), and the greatest error from using the direct proportionality equation (Fig. 8, method 1, SS=1.6711). When only the last annulus was used, the least error resulted from direct substitution into the fitted quadratic equation (Fig. 9, method 19, SS=0.0662), and the greatest error from using direct substitution into the OLS regression equation (Fig. 9, method 12, SS=1.5882).

### Asymptotically shaped OR-TL relation

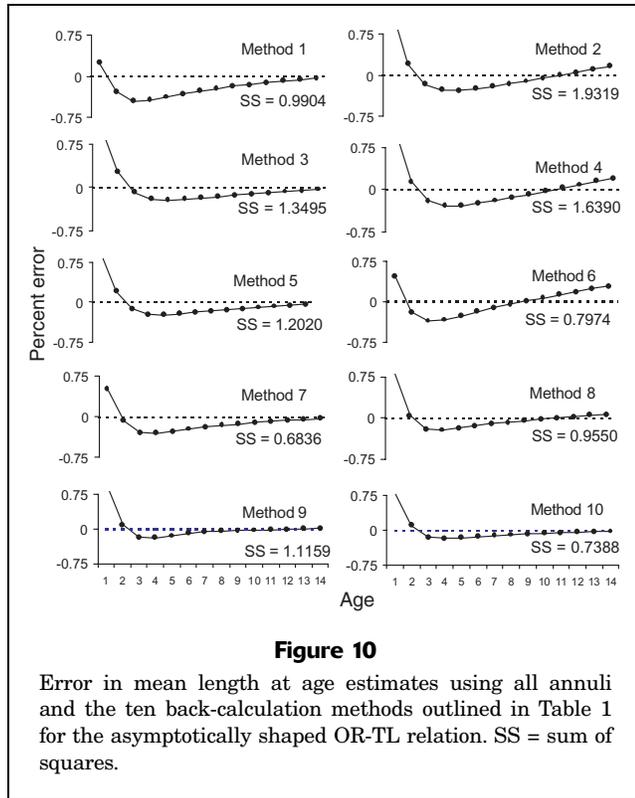
Of the four functions fitted to OR-TL/ASYM, the quadratic equation resulted in the highest coefficient of determination ( $r^2=0.963$ ); however the coefficient of determination of the Weibull function fit was nearly as high ( $r^2=0.958$ ).

As with the exponentially shaped OR-TL relation, when linear regression was used to model the OR-TL relation, the percent error by age followed the trend of residuals for the residuals for the regression (Fig. 10). Using the last annulus only resulted in generally lower sums-of-squares, especially when the  $y$ -intercept was corrected for log transformation of the OR-TL relation used (Fig. 11).

When the OR-TL relation was asymptotically shaped and all annuli were used, the least error resulted from using the individually corrected Weibull cumulative distribution function (Fig. 10, method 10, SS=0.7388), and the greatest error from using direct substitution in to the OLS regression equation (Fig. 10, method 2, SS=1.9319). When only the last annulus was used, the least error again resulted from using the individually corrected Weibull cumulative distribution function (Fig. 11, method 20, SS=0.0516), and the greatest error from using direct substitution in to the OLS regression equation (Fig. 11, method 12, SS=1.9261).

### Discussion

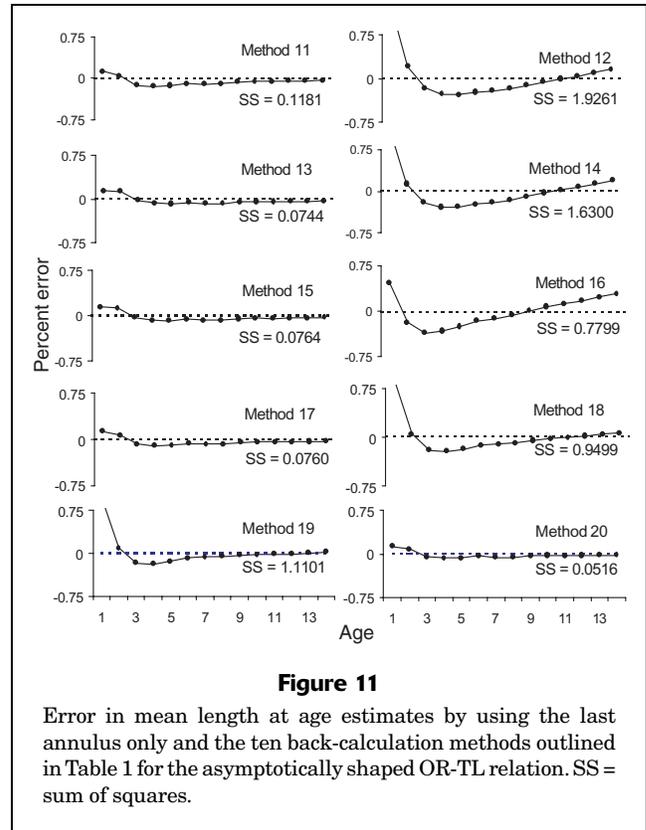
The most accurate estimates of length-at-age resulted from the best model fits of the OR-TL relation. Even though sampling was random, poorly fitted OR-TL regressions resulted in back-calculation tables with obvious "Lee's phenomenon" effects. Ricker (1969) pointed out that the use of an incorrect otolith radius-total length relationship can result in this effect. Smale and Taylor (1987) also



showed that using the improper back-calculation method can result in a false “Lee’s phenomenon” effect. Using only the last annulus reduced this effect with some back-calculation methods in this study, but not all of them. In general, the accuracy of the estimated length-at-age was directly related to how well the particular model fitted the OR-TL relation, suggesting that the OR-TL model is just as, if not more, important as selecting the appropriate back-calculation model.

Based on the importance of the fit of the OR-TL model, it follows that the methods used to sample the catch are of equal importance. Nonrandom samples of the catch, or length-based regulations that cause the catch to misrepresent the population, will affect the OR-TL regression. For instance, a minimum legal size will artificially truncate the OR-TL relation in samples of the catch and selectively sample faster-growing small fish. This could eliminate the youngest ages from the regression and could necessitate extrapolation of the regression beyond the range of the data. Furthermore, a truncation of the OR-TL regression would positively bias the  $y$ -intercept and lead to an overestimation of length-at-age, especially for the younger ages.

It has been pointed out that univariate statistical models, which assume independence of observations, are generally inappropriate for analysis of otolith increment data (Chambers and Miller, 1995). These authors have suggested that because otolith data constitute multiple measures, perhaps examination of the covariance is more appropriate than the comparison of individual means. In this study, however, I did not seek to emphasize the ex-



istence of (or lack of) a statistical difference between the true and estimated means sizes. Given the large sample sizes made available through simulation, conclusions of significant differences resulting from any statistical tests can be misleading. More useful, I believe, is the shape, direction, and magnitude of the biases that emerged from each back-calculation method. Consequently, I chose to emphasize the percent error between the true and estimated mean size-at-age. Using percent error allows more freedom of interpretation and is not subject to the problems associated with excessively large degrees of freedom of simulated data sets.

The individually corrected Weibull cumulative distribution function presented here proved to be very flexible and capable of accounting for the individual otolith radius-total length trajectories. This function is very similar to the linear  $y$ -intercept corrected back-calculation equation of Fraser-Lee but can accommodate a wide varieties of curvatures. The Weibull equation I reported (Eq. 13) has an origin at  $x$  and  $y$  of 0; however, a  $y$ -intercept term can easily be added to accommodate an OR-TL relation with a nonzero intercept.

Much of the cohort’s diversity in biological attributes was lost within the first few months of the life because of mortalities. By the time the cohort had completed one year of growth, the diversity in biological attributes of the individuals that would ultimately represent the cohort were established. Based on the observations of Secor and Houde (1995), the establishment of the biological attributes of a

cohort occurring after one year is a realistic representation of what occurs in the early life history of striped bass. Although the number of fish that a cell represented could be less than one, this number was used as a relative weighting to all other cells; thus, proportionally, the value was valid. Consequently, the actual starting number of fish of the cohort was irrelevant for this study but could be used to calibrate the model to a particular population of interest.

I was able to simulate a number of dissimilarly shaped OR-TL relationships by modifying the parameter used to convert brain weight to otolith weight from a constant to a function. However, trial runs showed that when this parameter was held constant, the resulting OR-TL relation was not linear. I later determined that because both soma and otolith growth were modeled as functions of weight and because the exponent of the weight-length equation (0.31) did not exactly equal the exponent of the equation that calculates the radius of a sphere (0.333), two rates must at some point diverge from linearity. For the purposes of this study, it was not necessary that the equations precisely depict the actual bioenergetics processes, only that true length of fish at annulus formation be known with certainty.

This study yields several conclusions important to studies of growth estimates from otolith back-calculations. The best back-calculation technique was directly related to how well the OR-TL model fitted. The percent error of any given method was rarely consistent across ages, although estimates of older ages were more accurate than those of younger ones. Younger ages were generally best estimated by using direct proportionality on the last annulus only. Thus, it may be necessary to use multiple methods to accurately estimate a growth curve. However, it would be difficult to select which combination of methods would be most accurate without prior knowledge of the true length-at-age.

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## Literature cited

- Bagenal, T.  
1978. Methods for assessment of fish production in fresh waters. IBP (International Biological Programme) Handbook 3, 3rd ed., 365 p. Blackwell Sci. Publ., Oxford.
- Brandt, S. B., and J. Kirsch.  
1993. Spatially explicit models of striped bass growth potential in Chesapeake Bay. *Trans. Am. Fish. Soc.* 122: 845–869.
- Chambers, R. C. and T. J. Miller.  
1995. Evaluating fish growth by means of otolith increment analysis: special properties of individual-level longitudinal data. *In* Recent developments in fish otolith research (D. H. Secor, J. M. Dean, S. E. Campana, eds.), p. 155–175. Univ. South Carolina Press, Columbia, SC.
- Cohen, J. E., S. W. Christensen, and C. P. Goodyear.  
1983. A stochastic age-structured population model of striped bass (*Morone saxatilis*) in the Potomac River. *Can. J. Fish. Aquat. Sci.* 40:2170–2183.
- Coutant, C. C., and D. L. Benson.  
1990. Summer habitat suitability for striped bass in Chesapeake Bay: reflections on a population decline. *Trans. Am. Fish. Soc.* 119:757–778.
- Coutant, C. C., K. L. Zachman, D. K. Cox, and B. L. Pearman.  
1984. Temperature selection by juvenile striped bass in laboratory and field. *Trans. Am. Fish. Soc.* 113:666–671.
- Francis, R. I. C. C.  
1990. Back-calculation of fish lengths: a critical review. *J. Fish Biol.* 36:883–902.
- Goodyear, C. P.  
1984. Analysis of potential yield per recruit for striped bass produced in Chesapeake Bay. *North Am. J. Fish. Manage.* 4:488–496.  
1985. Relation between reported commercial landings and abundance of young striped bass in Chesapeake Bay, Maryland. *Trans. Am. Fish. Soc.* 114:92–96.  
1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *In* Risk evaluation and biological reference points for fisheries management (S. J. Smith, J. J. Hunt, and D. Rivard, eds.), p. 76–81. *Can. Spec. Publ. Fish. Aquat. Sci.* 120.
- Gulland, J. A., and L. K. Borerema.  
1973. Scientific advice on catch levels. *Fish. Bull.* 71:325–335.
- Grimes, C. B.  
1978. Age, growth, and length-weight relationship of vermilion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina. *Fish. Bull.* 78:137–146.
- Hales, L. S., Jr., and K. W. Able.  
1995. Effects of oxygen concentration on somatic and otolith growth rates of juvenile black sea bass, *Centropristis striata*. *In* Recent developments in fish otolith research (D. H. Secor, J. M. Dean, and S. E. Campana eds.), p. 135–153. Univ. South Carolina Press, Columbia, SC.
- Heidinger, R. C., and K. Clodfelter.  
1987. Validity of the otolith for determining age and growth of walleye, striped bass, and smallmouth bass in power plant cooling ponds. *In* Age and growth of fish (R. C. Summerfelt and G. E. Hall, eds.), p. 241–251. Iowa State University Press, Ames, IA.
- Laws, L. A., and J. W. Archie.  
1981. Appropriate use of regression analysis in marine biology. *Mar. Biol.* 65:13–16.
- Milicich, M. J., and J. H. Choat.  
1992. Do otoliths record changes in somatic growth rates? Conflicting evidence from a laboratory and field study of a temperate reef fish, *Parika scaber*. *Aust. J. Mar. Freshwater Res.* 43:1203–1214.
- Mosegaard, H., H. Svedang, and K. Taberman.  
1988. Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of difference in temperature response. *Can. J. Fish. Aquat. Sci.* 45:1514–1524.
- Reznick D., E. Lindbeck, and H. Bryga.  
1989. Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). *Can. J. Fish. Aquat. Sci.* 46:108–112.
- Ricker, W. E.  
1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production and yield. *J. Fish. Res. Board Can.* 26:479–541.

1973. Linear regressions in fishery research. *J. Fish. Res. Board Canada* 30:343–409.
1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191, 382 p.
1992. Back-calculation of fish lengths based on proportionality between scale and length increments. *Can. J. Fish. Aquat. Sci.* 49:1018–1026.
- Rose K. A., S. W. Christensen, and D. L. DeAngelis.  
1993. Individual-based modeling for populations with high mortality: a new method based on following a fixed number of model individuals. *Ecol. Modeling* 68:273–292.
- Rose K. A., and J. C. Cowan.  
1993. Individual-based model of young-of-the-year striped bass population dynamics. I. Model description and baseline simulations. *Trans. Am. Fish. Soc.* 122:415–438.
- Rutherford, E. S., and E. D. Houde.  
1995. The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in Chesapeake Bay. *Fish. Bull.* 93:315–332.
- SAS (SAS Institute, Inc.).  
1988. SAS/STAT user's guide, release 6.03 ed., 1028 p. SAS Institute, Inc., Cary, NC.
- Schirripa, M. J., and C. P. Goodyear.  
1997. Simulation of alternative assumptions of fish otolith-somatic growth with a bioenergetics model. *Ecol. Modeling* 102:209–223.
- Secor, D. H.  
1992. Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay striped bass, *Morone saxatilis*. *Fish. Bull.* 90:798–806.
- Secor D. H., and J. M. Dean.  
1989. Somatic growth effects on the otolith—fish size relationship in young pond-reared striped bass, *Morone saxatilis*. *Can. J. Fish. Aquat. Sci.* 46:113–121.
1992. Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis*. *Can. J. Fish. Aquat. Sci.* 49:1439–1454.
- Secor D. H., and E. D. Houde.  
1995. Temperature effects on the timing of striped bass egg production, larval viability, and recruitment potential in the Patuxent River (Chesapeake Bay). *Estuaries* 18(3): 527–544.
- Smale, M. A., and W. W. Taylor.  
1987. Sources of back-calculation error in estimating growth of lake whitefish. *In* Age and growth of fish (R. C. Summerfelt and G. E. Hall, eds.), p. 189–202. Iowa State Univ. Press, Ames, IA.
- Tuncer, H.  
1988. Growth, survival, and energetics of larval and juvenile striped bass (*Morone saxatilis*) and its white bass hybrid (*M. saxatilis* × *M. chrysops*). M.S. thesis, 136 p. Univ. Maryland, College Park, MD.
- Weibull, W.  
1951. A statistical distribution function of wide applicability. *J. Appl. Mechanics* 18:293–297.
- Wright, P. J., N. B. Metcalfe, and J.E. Thorpe.  
1990. Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L: evidence against coupling. *J. Fish. Biol.* 36:241–249.
- Vaughan, D. S., and M. L. Burton.  
1994. Estimation of von Bertalanffy growth parameters in the presence of size-selective mortality: a simulated example with red grouper. *Trans. Am. Fish. Soc.* 123:1–8.